Cortical Regions Associated with Perceiving, Naming, and Knowing about Colors

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Abstract

■ Positron emission tomography (PET) was used to investigate whether retrieving information about a specific object attribute requires reactivation of brain areas that mediate perception of that attribute. During separate PET scans, subjects passively viewed colored and equiluminant gray-scale Mondrians, named colored and achromatic objects, named the color of colored objects, and generated color names associated with achromatic objects. Color perception was associated with activations in the lingual and fusiform gyri of the occipital lobes, consistent with previous neuroimaging and human lesion studies. Retrieving information about object color (generating color names for achromatic objects relative to naming achromatic objects) activated the left inferior temporal, left frontal, and left posterior parietal cortices, replicating previous findings from this laboratory. When subjects generated color names for ach-romatic objects relative to the low-level baseline of viewing gray-scale Mondrians, additional activations in the left fusiform/lateral occipital region were detected. However, these activations were lateral to the occipital regions associated with color perception and identical to occipital regions activated when subjects simply named achromatic objects relative to the same low-level baseline. This suggests that the occipital activations associated with retrieving color information were due to the perception of object form rather than to the top-down influence of brain areas that mediate color perception. Taken together, these results indicate that retrieving previously acquired information about an object's typical color does not require reactivation of brain regions that subserve color perception. ■

INTRODUCTION

Does retrieving previously stored information about an attribute of an object depend on reactivating brain regions that mediate perception of that attribute? The notion that visual imagery engages the top-down activation of representations that are also active during perception dates at least as far back as the philosophical writings of Hume (Hume, 1739/1969). Today, visual neuroscientists still debate whether the cortical areas that subserve visual imagery are identical to those that underlie visual perception. One side maintains that visual imagery and visual perception are mediated by a common neural substrate that includes early visual areas (Goldenberg et al., 1989; Kosslyn et al., 1993; Kosslyn, Thompson, Kim, & Alpert, 1995; Le Bihan et al., 1993), and the other side argues that visual imagery does not involve early visual areas but rather high-level visual areas only (Behrmann, Winocur, & Moscovitch, 1992; Charlot, Tzourio, Zilbovicius, Mazoyer, & Denis, 1992; Decety, Kawashima, Gulyas, & Roland, 1992; D'Esposito et al., 1997).

Consistent with this latter view, recent studies of patients with focal brain lesions suggest that perception of a purely visual feature (i.e., color) and imagery for that feature may be differentially impaired. For example,

there have been reports of patients with preserved color perception and impaired color imagery (De Vreese, 1991) and, conversely, of an achromatopsic patient with intact color imagery (Shuren, Brott, Schefft, & Houston, 1996). Given that imagery relies on previously organized and stored information (i.e., knowledge about the features being imagined; Kosslyn, Thompson, & Alpert, 1997), these reports suggest that the neural network that subserves color knowledge may be anatomically dissociable from the one that subserves color perception. Nevertheless, the possibility remains that, in the normal intact brain, retrieving information about object color may entail the top-down influence of brain regions where color information is stored upon areas subserving color perception.

Using positron emission tomography (PET), Martin, Haxby, Lalonde, Wiggs, and Ungerleider (1995) reported activations in a region of the ventral temporal lobe anterior to previously reported color perception areas when subjects retrieved previously acquired information about an object's color. Although this result seems to support an anatomical distinction between color perception and color knowledge, the cortical regions that mediate color perception were not identified in that study. Also, the color information retrieval condition was compared to a baseline task (naming achromatic objects)

that has been shown to elicit occipital cortex activity (Bookheimer, Zeffiro, Blaxton, Gaillard, & Theodore, 1995; Kiyosawa et al., 1996; Martin, Wiggs, Ungerleider, & Haxby, 1996). Even if retrieving previously acquired color information reactivated the cortical regions that mediate color perception, any activity in color perception regions in the occipital cortex could have been obscured or eliminated when contrasted with an object naming baseline. For these reasons, the precise relationship between the neural circuitry associated with color perception and color knowledge remains to be clarified.

For the current study, color knowledge refers to previously acquired information about the prototypical colors of objects. Color knowledge is not arbitrary because most people have shared ideas about the typical colors for objects (Joseph & Proffitt, 1996). For example, adults can readily judge the extent to which particular colors are characteristic of various objects, suggesting that information about the typical colors of objects is represented in memory (Siple & Springer, 1983).

The goal of the current study was to investigate whether retrieving previously acquired information about an object's color requires reactivation of brain areas that mediate perception of color. We used PET to identify the functional neuroanatomy associated with color perception, color naming, and color knowledge within a single group of subjects.

During separate scans, subjects were presented with colored and equiluminant gray-scale Mondrians (Land, 1974), appropriately colored objects embedded within colored Mondrians, and achromatic objects embedded within gray-scale Mondrians (see Figure 1). Subjects passively viewed the colored and gray-scale Mondrians. In addition, subjects performed four verbal tasks: They named the colored and achromatic objects, they named the color of colored objects, and they generated color names commonly associated with achromatic objects.

RESULTS

Behavioral Performance

Mean response accuracy and voice onset times (VOTs) for the 50 stimuli presented during each condition of the verbal tasks are shown in Table 1. Errors were relatively rare and did not differ significantly across the four conditions. As expected, VOT differed significantly across conditions ($F(3, 33) = 60.4$, $p < 0.0001$). Subjects were faster at naming the colors of colored objects ($F(1, 33) = 12.4$, $p < 0.005$) and slower at generating color names associated with achromatic objects ($F(1, 33) = 117.6$, $p < 0.0001$) compared to both naming colored objects and naming achromatic objects. VOT for the two object naming conditions did not differ from each other ($p > 0.10$).

The mean proportion of subjects who retrieved the same color names for the same objects was 76% (range:

Table 1. Mean Accuracies and VOTs

Task	Accuracy (% correct)		Voice onset time (msec)	
	Mean	*SD*	*Mean*	*SD*
Naming colored objects	95.18	3.47	779.25	52.91
Naming achromatic objects	93.67	5.53	769.93	93.87
Naming color	98.38	2.29	705.98	53.59
Generating color names	95.81	5.96	986.14	92.29

33 to 100%). For example, 9 out of the 12 subjects responded "yellow" to the achromatic bulldozer depicted in Figure 1. In addition, subjects were also consistent in their responses; the mean within-subject agreement for color naming of the objects was 80% (range: 63 to 91%).

Rationale for Comparisons of Regional Cerebral Blood Flow (rCBF) Data

To determine the relationship between brain regions associated with perceiving color and those associated with retrieving previously acquired information about object color, the following comparisons were performed: First, the areas of the occipital cortex associated with color perception were identified. This was accomplished by contrasting pairs of conditions that differed only with regard to the presence of color in one condition but not in the other. These paired conditions were viewing colored versus viewing gray-scale Mondrians and naming colored objects versus naming achromatic objects. Next, regions of the occipital cortex associated with object identification, but not color perception, were identified by comparing the achromatic object naming condition to the low-level baseline condition (passively viewing the gray-scale Mondrians).

Having identified occipital regions differentially associated with the perception of color and the perception of object form, we next addressed the central question motivating this study: Does retrieving information about object color require reactivation of areas that mediate perception of color? This was done by contrasting the condition where subjects generated color names for achromatic objects with the condition where subjects named achromatic objects. This comparison would determine whether the pattern of activation associated with the retrieval of color knowledge was the same as previously reported. However, as previously discussed, naming achromatic objects has been shown to elicit activity in the occipital cortex. As a result, this baseline

could obscure or eliminate occipital activity associated with retrieving previously acquired color information. For this reason, the generating color names condition was also compared with a low-level baseline condition (viewing gray-scale Mondrians). This was the same baseline used in the comparisons to determine regions of the occipital cortex associated with color perception and object identification described above. The location of the activations revealed by this comparison would determine if the areas of the occipital cortex active when subjects retrieved previously acquired color information were the same as those active when subjects perceived colors, or whether these occipital areas were associated with other aspects of the task (e.g., perception of object form).

Finally, the cortical areas associated specifically with color naming were determined by contrasting conditions where subjects named the color of colored objects with conditions where subjects named the colored objects.

Color Perception

Perception of color was associated with increased rCBF in the right lingual gyrus (BA 18) and the left fusiform gyrus (BA 37; see Figure 2). Additional activations were also revealed in the right precuneus (BA 31) and left superior parietal lobe (BA 7; see Table 2).

Object Identification

Brain regions associated with object identification, but not color perception, were identified by comparing the achromatic object naming condition to the low-level baseline condition (passively viewing the gray-scale Mondrians). This comparison revealed bilateral activation in the lingual/fusiform region of the occipital and posterior temporal lobes (BA 18, centered in the collateral sulcus, and BA 19) and fusiform gyrus of the left temporal lobe (BAs 36, 37; see Figure 3). Additional activations were in the right middle and superior temporal gyri (BA 21/22), cingulate gyrus (BA 32), left prefrontal lobe (BAs 9, 45), precentral gyrus (BA 4), and the cerebellum bilaterally; see Table 3.

Retrieving Previously Acquired Color Information

Relative to naming achromatic objects, generating the names of colors associated with achromatic objects produced activity in the left inferior temporal (BA 20), left parietal (BAs 7, 40), left frontal (BAs 6, 8, 11, 44, 46), and the cingulate (BA 23) regions. These results replicate previous findings from this laboratory (Martin et al., 1995; see Figure 4). This comparison also revealed activations in the right frontal lobe (BAs 6, 46). However, the occipital cortex was not active when subjects generated

Table 2. Local Maxima within Areas Demonstrating Greater rCBF for Passively Viewing Colored Mondrians and Naming Colored Objects than for Passively Viewing Gray-Scale Mondrians and Naming Achromatic Objects

Brain Region (Brodmann's Area)	Talairach Coordinates			Z score
	x	y	z	
Occipital lobe				
Right lingual gyrus (18)	4	−86	0	3.50
Temporal lobe				
Left fusiform gyrus (37)	−22	−56	−12	3.55
Parietal lobe				
Right precuneus cortex (31)	18	−58	24	3.30
Left superior parietal cortex (7)	−28	−70	36	3.17

color names relative to naming achromatic objects (see Table 4A and Figure 5A).

As previously mentioned, the lack of occipital activity was not surprising given that the baseline task used in this comparison (naming achromatic objects) would also be expected to produce activity in the occipital cortex. To identify occipital regions that might be active when subjects retrieved color knowledge, the generating color names condition was also compared to a low-level baseline condition (passively viewing gray-scale Mondrians). In addition to activations in the left inferior temporal, left frontal, and left parietal cortices, this second comparison revealed activations in the left fusiform and lingual gyri (BA 18) and the right lingual gyrus (BA 18) of the occipital cortex (see Table 4B and Figure 5B). The local maxima of these occipital activations did not overlap with the activations in the occipital cortex associated with color perception; rather they were approximately 2 cm lateral to the occipital activations associated with color perception. Also the activations in the left fusiform (−38, −76, −8), right fusiform (38, −64, −16), and right lingual (22, −86, −8) gyri were nearly identical to the posterior activations associated with naming achromatic objects relative to the same low-level baseline (left fusiform: −38, −76, −4; right fusiform: 36, −62, −16; right lingual: 20, −86, −8; compare Tables 4B and 3).

Color Naming

Brain regions active during color naming were identified by comparing scans where subjects named the color of colored objects with scans where subjects named colored objects. In this comparison, the stimuli were identical in both conditions, only the attribute to which
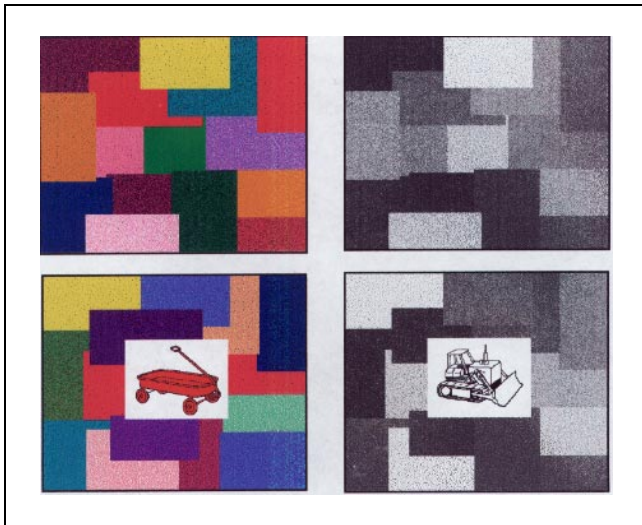
Figure 1. Examples of the stimuli used in the experiment. Subjects were instructed to passively view the colored and equiluminant grayscale Mondrians, to name the colored and achromatic objects embedded within the Mondrians (e.g., wagon and bulldozer), to name the color of the colored objects (e.g., red), and to generate color words associated with the achromatic objects (e.g., yellow).
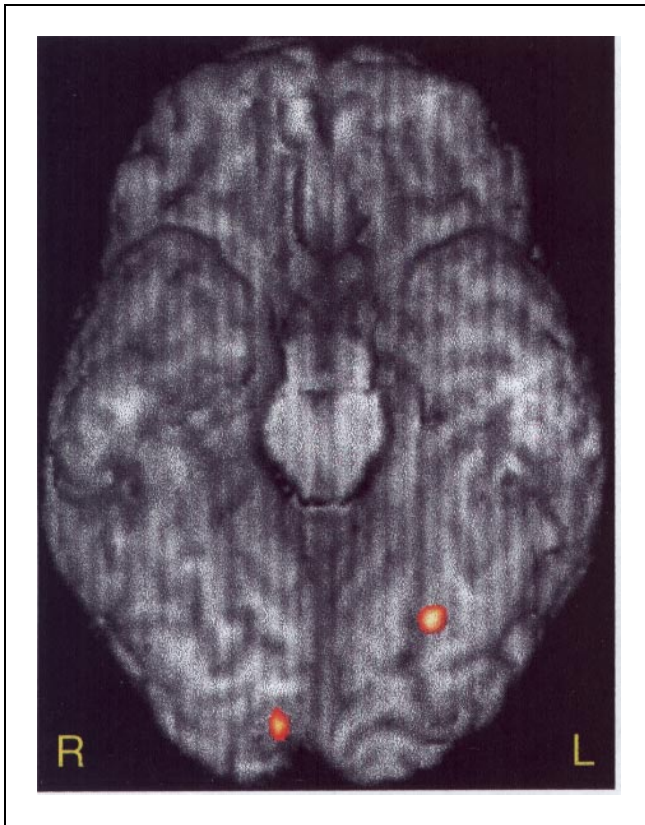

Figure 2. Activations associated with passive color perception: (passively viewing colored Mondrians + naming colored objects) > (passively viewing gray-scale Mondrians + naming achromatic objects). These activations are displayed as see-through ventral projections with Z-coordinates of 0 or lower, excluding the cerebellum. The local maxima of each activation exceeded a Z score threshold of 3.09. Activations were thresholded at $Z > 2.32$ for display purposes.
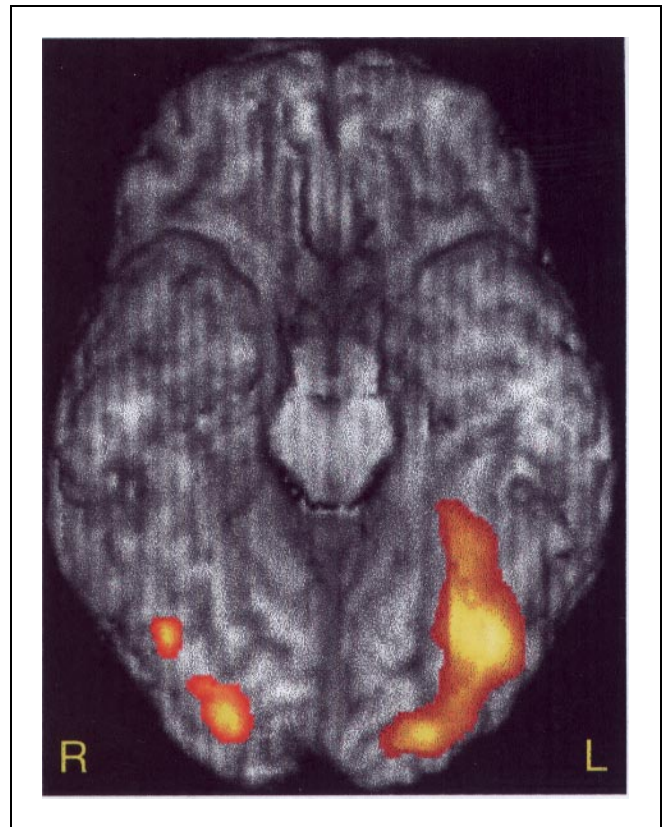

Figure 3. See-through ventral projection of activations ($Z > 3.09$) associated with object identification (naming achromatic objects > passively viewing gray-scale Mondrians).

subjects attended varied (e.g., responding "red" versus "wagon" to the presentation of a red wagon). Relative to naming colored objects, selectively attending to and naming the color of colored objects activated the left lingual gyrus (BA 18), close to the color perception region identified in previous studies (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991; Sakai et al., 1995; Zeki et al., 1991), and the right inferior temporal lobe (BA 20), close to the region active when subjects retrieved previously acquired information about object color in a prior study (Martin et al., 1995; see Table 5 and Figure 6). There was an additional activation in the left inferior temporal lobe close to the region associated with retrieving color information identified in the current as well as previous studies (Martin et al., 1995; Wiggs, Weisberg, & Martin, in press) when the threshold was lowered to $Z > 2.32$ ($p < 0.01$, one-tailed).

Although generating color names to achromatic objects and naming the colors of colored objects both produced activity in the left inferior temporal lobe, a direct comparison of the two conditions revealed that the left inferior temporal lobe was markedly more active when subjects retrieved color knowledge (i.e., generated color names to achromatic objects) than when they named the color of colored objects (−56, −40, −12; $Z = 3.97$).

Table 3. Local Maxima within Areas Demonstrating Greater rCBF for Naming Achromatic Objects than for Passively Viewing Gray-Scale Mondrians

Brain Region (Brodmann's Area)	Talairach Coordinates			Z score
	x	y	z	
Occipital lobe				
Left fusiform gyrus (18)	−38	−76	−4	5.24
Left lingual gyrus (18)	−24	−88	−4	5.12
Left fusiform gyrus (19)	−30	−62	−16	5.64
Right lingual gyrus (18)	20	−86	−8	4.51
Right fusiform gyrus (19)	36	−62	−16	4.69
Temporal lobe				
Left fusiform gyrus (37/36)	−32	−36	−20	4.42
Right middle/superior temporal gyrus (21/22)	42	−36	4	4.69
Frontal lobe				
Left middle frontal region (9)	−26	42	28	4.73
Left inferior frontal gyrus (45)	−40	22	12	5.68
Left precentral gyrus (4)	−44	−12	40	7.45
Right precentral gyrus (4)	50	−8	32	4.93
Cingulate gyrus (32)	0	6	44	6.83
Cerebellum				
Left	−12	−62	−20	5.37
Right	12	−66	−24	6.10

DISCUSSION

Color Perception

Consistent with previous neuropathological findings that achromatopsia in humans is commonly associated with lesions in the lingual and fusiform gyri (Zeki, 1990), color perception produced activations in the lingual and fusiform gyri of the occipital lobe in the current study. The location of these occipital activations is also consistent with studies of color perception using electrophysiological recordings (Allison et al., 1993; Buchner, Weyen, Frackowiak, Romaya, & Zeki, 1994; Plendl et al., 1993), PET (Corbetta et al., 1991; Zeki et al., 1991) and functional magnetic resonance imaging (Clark et al., 1997; Sakai et al., 1995). Having successfully identified regions of the occipital cortex associated with color perception, we next examined whether these regions were also active when subjects retrieved previously acquired information about colors.
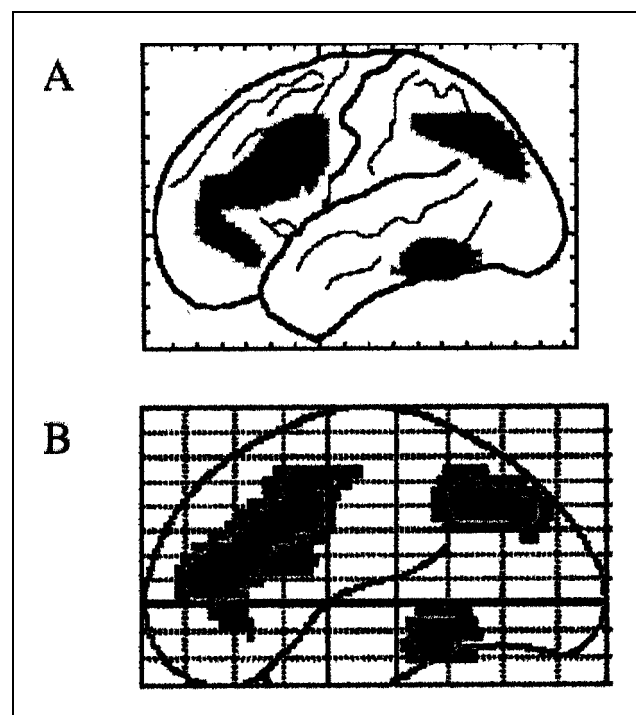

Figure 4. See-through lateral projection of activations associated with retrieving color knowledge relative to naming achromatic objects. A: adapted from Martin et al., 1995. B: data from the current study.

Retrieving Previously Acquired Color Information

When subjects were instructed to retrieve previously acquired color information (generating color names associated with achromatic objects), there were activations in the left inferior temporal, left parietal, and left frontal regions in comparison to activity associated with a high-level baseline (naming achromatic objects), replicating previous results from this laboratory (Martin et al., 1995; Wiggs et al., in press). Additional activations were revealed in the fusiform gyrus, bilaterally, and in the right lingual gyrus of the occipital cortex when the generating color names condition was contrasted with a low-level baseline (passively viewing gray-scale Mondrians). However, the location of these activations is not consistent with the idea that retrieving previously acquired information about object color requires reactivating areas involved with color perception. First, these occipital activations did not overlap with the activations related to color perception found in this study and other reports in the literature; rather they were approximately 2 cm lateral to the activations associated with color perception. Second, the location of these occipital activations was identical to the activations associated with naming achromatic objects relative to the same low-level baseline task. Previous studies of object perception and object naming have shown that the fusiform/lateral occipital region is activated by pictures of real objects

Table 4A. Local Maxima within Areas Demonstrating Significantly Greater rCBF for Generating Color Names Relative to Naming Achromatic Objects

Brain Region (Brodmann's Area)	Talairach Coordinates			Z score
	x	y	z	
Temporal lobe				
Left inferior temporal gyrus (20)	−52	−36	−12	6.53
Parietal lobe				
Left superior parietal region (7)	−30	−68	36	5.44
Left inferior parietal region (7)	−36	−58	36	5.29
Left inferior parietal region (40)	−38	−52	40	5.42
Frontal lobe				
Left superior frontal gyrus (6)	−26	6	48	4.97
Left middle frontal sulcus (46)	−40	34	16	5.72
Left middle frontal region (46)	−36	44	8	5.62
Left middle frontal gyrus (8)	−38	14	36	5.42
Left inferior frontal gyrus (44)	−50	8	12	3.67
Left orbital frontal region (11)	−28	36	−8	4.17
Left medial frontal gyrus (6)	−10	12	48	3.95
Right middle frontal region (46)	30	38	16	3.60
Right middle frontal region (6)	28	12	40	3.09
Right inferior frontal region (46)	42	6	28	3.58
Left cingulate gyrus (32)	−2	14	40	3.58
Cerebellum				
Left	−40	−68	−20	3.26

Table 4B. Local Maxima within Areas Demonstrating Significantly Greater rCBF for Generating Color Names Relative to Passively Viewing Gray-Scale Mondrians

Brain Region (Brodmann's Area)	Talairach Coordinates			Z score
	x	y	z	
Occipital lobe				
Left fusiform gyrus (18)	−38	−76	−8	6.02
Right fusiform gyrus (19)	38	−64	−16	3.48
Right lingual gyrus (18)	22	−86	−8	5.06
Temporal lobe				
Left inferior/middle temporal gyrus (20/21)	−56	−36	−4	4.07
Right medial temporal region	36	−36	0	4.00
Parietal lobe				
Left superior parietal region (7)	−22	−68	40	4.06
Left inferior parietal region (7)	−34	−54	40	4.36
Frontal lobe				
Left superior frontal gyrus (6)	−32	8	48	3.52
Left middle frontal region (46)	−32	42	20	6.08
Left inferior frontal gyrus (45)	−40	22	20	6.79
Left precentral gyrus (6)	−46	0	24	7.31
Left precentral gyrus (4)	−44	−12	40	6.11
Left cingulate gyrus (32)	−2	8	44	7.98
Left insula	−34	18	4	5.90
Right insula	28	14	4	3.81
Subcortical				
Left thalamus	−16	−20	8	3.59
Cerebellum				
Left	−32	−62	−20	6.56
	−6	−60	−20	5.09
Right	20	−66	−24	5.80
	2	−58	−24	5.12

and pictures of nonsense object forms (Malach et al., 1995; Martin et al., 1996), suggesting that this region is involved in the perception of object form, regardless of meaning. Furthermore, the coordinates of these object-form-related activations (Malach et al., 1995: 43, −73, −18; Martin et al., 1996: −38, −82, 4 and 34, −72, −8) were nearly identical to the coordinates of the occipital activations obtained when subjects generated color names to achromatic objects relative to passively viewing gray-scale Mondrians in the current study (−38, −76, −8 and 38, −76, −4). Thus, the most likely explanation for these occipital lobe activations is that they were related to the initial perceptual encoding of the achromatic objects presented during the scans and not to the top-down reactivation of regions mediating color perception.

The objects chosen for the current study were all manufactured items whose color is determined by social convention (e.g., a red wagon and a yellow bulldozer). Because the color of such entities is somewhat arbitrary, it has been proposed that persons typically must imagine the items in color before they can correctly generate the associated prototypical color names (De Vreese, 1991; Farah, 1984). However, it should be noted that the generating color names task used in the current study was
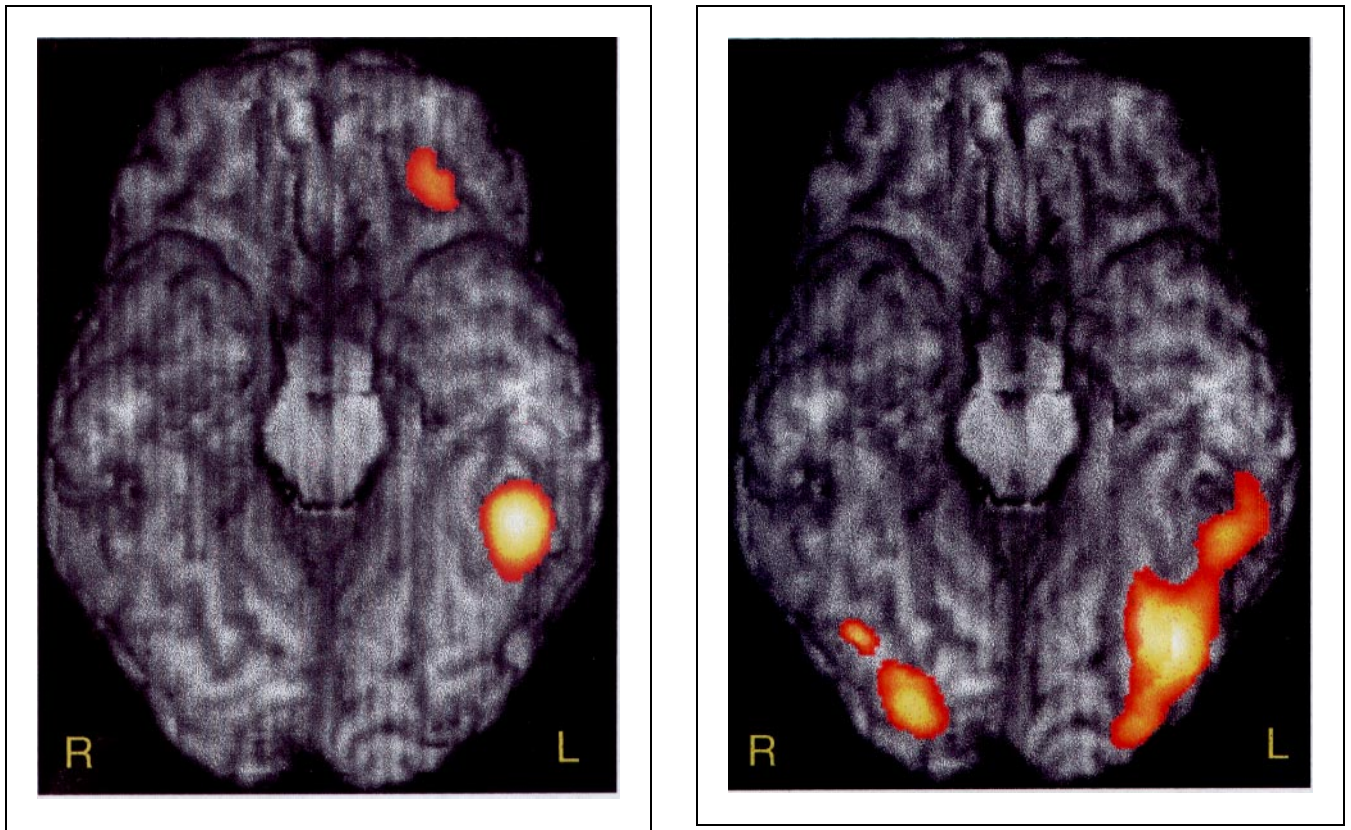
Figure 5. See-through ventral projection of activations ($Z > 3.09$) associated with retrieving previously acquired information about object color. A: (generating color names associated with achromatic objects > naming achromatic objects). B: (generating color names associated with achromatic objects > passively viewing gray-scale Mondrians).

not a mental imagery task per se. Subjects were instructed to come up with color names commonly associated with the achromatic objects that they saw; they were neither encouraged nor discouraged to use mental imagery. Debriefing after the experimental sessions revealed that only a few subjects were conscious of employing imagery techniques and none of these subjects reported that they used mental imagery consistently throughout the task. Nevertheless, given that mental imagery relies on the ability to retrieve previously organized and stored information (Kosslyn et al., 1997), the current finding that retrieving previously acquired information about object color does not reactivate the brain regions that mediate color perception is consistent with the finding that the primary visual cortex is not engaged during mental imagery (D'Esposito et al., 1997; Mellet et al., 1993).

Figure 6. See-through ventral projection of activations associated with color naming (naming the color of colored objects > naming colored object). To display the activation in the left inferior temporal lobe, the local maxima of the activations in this figure were thresholded at $Z > 2.32$.
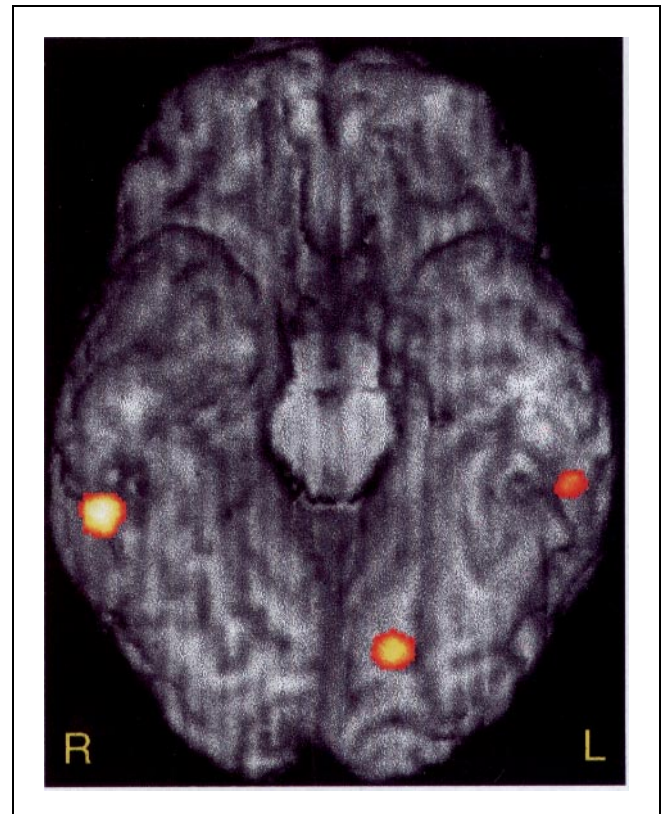
Table 5. Local Maxima within Areas Demonstrating Significantly Greater rCBF for Naming the Color of Colored Objects than for Naming Colored Objects

Brain Region (Brodmann's Area)	Talairach Coordinates			Z score
	x	y	z	
Occipital lobe				
Left lingual gyrus (18)	−12	−74	0	3.15
Temporal lobe				
Right inferior temporal gyrus (20)	52	−40	−16	3.38
Left inferior temporal lobe (20)	−52	−34	−16	2.75
Parietal lobe				
Left inferior parietal region (7)	−34	−60	36	4.98
Frontal lobe				
Left superior frontal region (6)	−22	12	48	3.58
Left middle frontal region (9)	−36	24	28	3.38

Naming Colors and Stored Information about Colors

Color naming denotes the retrieval of the lexical form (or name) that refers to a particular color. Patients who suffer from color anomia may perceive and recognize colors normally and yet be unable to name them correctly.

In the current study, naming the color of colored objects, relative to naming colored objects, elicited activity in the left lingual gyrus of the occipital lobe and in the inferior temporal cortex bilaterally. The locations of these activations were nearly identical to the regions associated with color perception (lingual gyrus) and retrieving color knowledge (inferior temporal cortex) in the current study, as well as in previous reports (color perception: Clark et al., 1997; Corbetta et al., 1991; Sakai et al., 1995; Zeki et al., 1991; color knowledge: Martin et al., 1995; Wiggs et al., in press). The fact that color perception areas were active is consistent with previous studies showing that selective attention to an object feature, such as color, results in increased activity in regions that mediate perception of that feature (e.g., Corbetta et al., 1991). Thus, these results indicate that naming the colors of colored objects engages brain regions that mediate color perception, as well as those associated with retrieving previously acquired color information.

Because subjects responded with the names of colors during the generating color names condition and the color naming condition, it could be argued that the activations in the inferior temporal regions elicited when subjects generated color names was not due to the retrieval of color information per se but rather to the retrieval of lexical form. This hypothesis, however, is unlikely for the following reasons. First, the left inferior temporal lobe was considerably more active when subjects generated color names than when they named colors. Second, subjects were slower to generate color names than to name colors, suggesting that subjects worked harder when generating color names and that this extra work involved retrieving previously acquired information about object color. This assertion is further supported by the high degree of between-subject agreement on the color names assigned to the achromatic objects (on average, 76% of subjects retrieved the same color name for each object). Thus, the data strongly suggest that when subjects generated color names associated with achromatic objects, they retrieved previously acquired information about the colors in which the objects normally appear, not simply random color names.

Additional evidence suggesting that the inferior temporal region may be the site for stored information about object color comes from a PET study of word-color synesthetes (individuals who experience color images when they hear words; Paulesu et al., 1995). In that study, it was found that auditory presentation of words activated the left inferior temporal cortex in the synesthetes but not in normal control subjects. The location of the left inferior temporal activation in the synesthetes (−50, −42, −12) was nearly identical to the location of the left inferior temporal activation associated with retrieval of color knowledge in the current study (−52, −36, −12). The close correspondence between the location of activity when synesthetes experienced color images and when normal subjects retrieved previously acquired color information provides compelling converging evidence that this region of the inferior temporal cortex is the site of stored color information. In addition, the fact that synesthetes did not have to retrieve color words suggests that activity in the inferior temporal cortex does not depend on the overt retrieval of color word forms. Finally, with regard to the relationship between perception and knowledge, it is noteworthy that although the synesthetes experienced color when they heard words, the posterior regions of the occipital cortex were not active. Thus, it appears that even vivid experience of color images does not require the reactivation of areas that mediate color perception.

CONCLUSION

Retrieval of information about a specific object attribute does not require reactivation of brain areas that mediate perception of that attribute. Relative to a low-level baseline, retrieving previously acquired color information elicited activations in the occipital cortex. However, rela-

tive to the same low-level baseline, naming achromatic objects also produced robust blood flow increases in the same areas of occipital cortex. Based on regions identified in the current study that responded selectively to color and not to object form, our results indicate that the cortical areas that subserve color knowledge are distinct from the cortical areas that subserve color perception. In contrast, naming the color of colored objects engaged not only color perception areas but areas associated with the storage of color information as well.

METHODS

Subjects

Twelve (six males) healthy, right-handed subjects, with a mean age of 28.8 years (*SD* 5.6), participated in the study. All subjects were of normal intelligence as measured by the American version of the Nelson Adult Reading Test (AMNART; Grober & Sliwinski, 1991; mean = 118; range 111 to 128). All subjects gave written informed consent.

Experimental Procedure

The stimulus presentation parameters were identical to those used by Martin et al., (1995). A total of 155 different objects, most selected from the Snodgrass and Vanderwart (1980) set, were used in the study. A fixed set of 35 colored objects (red, orange, yellow, light green, dark green, light blue, dark blue, purple, pink, brown, tan, black, gray, or white) and a fixed set of 35 achromatic objects occurred in random order at the beginning and end of the verbal conditions (first 13 and last 22). The first fixed set of objects served as a buffer to engage subjects in the desired mode of processing. In addition, both fixed sets of achromatic objects were used to obtain data on within- and between-subject response consistency for the generating color names condition. Fifteen objects intervened between the fixed sets of objects during each scan. The presentation of these 15 objects coincided with the critical first 30 sec of the 60-sec scan (Hurtig et al., 1994). These objects, seen by subjects only once during the experiment, consisted of manufactured objects whose typical color is determined by social convention (e.g., a red wagon and a yellow bulldozer).

Eight 15-item lists were constructed. All the objects in these lists were equated for name frequency (Kucera & Francis, 1967), categories, and category typicality ranking (Battig & Montague, 1969). In addition, the colored and achromatic objects were counterbalanced such that what one subject saw in color another would see in black and white.

Approximately 24 hours prior to the scanning sessions, subjects were familiarized with the four verbal tasks. A list of 80 objects, different from those presented during the scanning sessions, were selected to serve as practice stimuli during training.

PET Scanning

Fifty stimuli were presented during each scan. The colored and gray-scale Mondrians were always presented during the first and last scans of each session, counterbalanced across subjects. Two scans each were obtained for the four verbal conditions, counterbalanced in a block design across subjects. A Macintosh IIfx computer using SuperLab software (Cedrus, Wheaton, MD; Haxby, Parasuraman, Lalonde, & Abboud, 1993) presented the stimuli and recorded subjects' VOTs. All stimuli were presented for 180 msec, followed by a centrally located fixation cross for 1820 msec. Stimuli were presented on a computer monitor positioned approximately 60 cm from the subject's eyes and tilted to be perpendicular to the subject's line of sight.

The rCBF was measured with a Scanditronix PC2048-15B tomograph (Milwaukee, WI), which acquired 15 contiguous, cross-sectional images simultaneously. Within-plane resolution was 6.5 mm (full width at half-maximum). Head movement was minimized by using a thermoplastic mask that was molded to the subject's head and attached to the scanner bed. Subjects began the task approximately 30 sec before injection of 30 mCi of $H_2^{15}O$. Scanning began when the brain radioactivity count reached a threshold value and continued for 60 sec thereafter.

Data Analysis

Voxel dimensions in the original scans were $2 \times 2 \times 6.5$ mm. Using linear interpolation, scans were converted to 43-slice images with $2 \times 2 \times 2.27$ mm voxels. Alignment of a selected scan in the y (anterior/posterior) and z (superior/inferior) dimensions was rectified using a maximum zero-crossover method (Minoshima, Berger, Lee, & Mintun, 1992). The remaining scans were aligned to the rectified first scan using an iterative procedure that also tested fit using the maximum zero-crossover method (Lee, Berger, & Mintum, 1991) and found the optimum alignment by iterating seven parameters (scale and six movements: roll, pitch, yaw, x-translation, y-translation, z-translation) with the simplex search algorithm (Nelder & Mead, 1965). These procedures, implemented on an Intel iPSC860 parallel supercomputer, corrected all scans for roll, yaw, and between-scan head movements.

Task-related differences in rCBF were tested using statistical parametric mapping ("Classic SPM"; Friston, Frith, Liddle, & Frackowiak, 1991a, 1991b; Friston et al., 1990; Friston et al., 1989; Friston, Worsley, Frackowiak, Mazziotta, & Evans, 1994). SPM consists of stereotactic normalization, correction for global flow, and task comparisons. Stereotactic normalization is a fully automated

procedure that scales each scan to the dimensions of the Talairach and Tournoux (1988) stereotactic brain atlas, aligns the scan to the estimated location of the line connecting the anterior and posterior commissures, and reshapes the scan, using nonlinear resampling, to the conformation of a template PET scan. Stereotactic normalization resamples each scan into voxels that are $2 \times 2 \times 4$ mm in the x, y, z planes, respectively. The scans were smoothed using a Gaussian filter with a full width at half-maximum of 1.2 cm in $x, y,$ and z. After each individual's scan had been reassembled to a standard brain coordinate space, statistics were calculated for each voxel sampled in all subjects. The rCBF for each voxel was corrected for variations in global blood flow by dividing each voxel value by the global mean for that scan. The significance of the rCBF differences between sets of task conditions was tested by calculating t tests using the pooled estimate of error variance. Values of t were converted to standard Z values to provide a measure of statistical significance that is independent of sample size. Changes in rCBF were defined as significant at a threshold of $Z > 3.09$ ($p < 0.001$, one-tailed) unless otherwise indicated.

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